

Iago, A NEW GENUS OF CARCHARHINID SHARKS, WITH A REDESCRIPTION OF *I. omanensis*

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ABSTRACT

A new genus, *Iago*, is proposed for *Eugaleus omanensis* Norman, 1939. *I. omanensis*, originally described from a single specimen, is redescribed from 16 additional specimens from the northern Arabian Sea continental shelf and slope between the Gulf of Oman and the Gulf of Kutch. Its presence in areas of low oxygen and the possibility of its occurrence in deeper waters of the Red Sea are discussed.

Norman (1939) described *Eugaleus omanensis* from a 280-mm female specimen, taken at 210-m depth in the Gulf of Oman. He placed it in *Eugaleus* Gill, 1864 (= *Galeorhinus* Blainville, 1816) with reservations because *omanensis* differed from all other species of *Eugaleus* in dentition and absence of a pronounced ventral caudal lobe. Norman noted that *omanensis* did not fit *Hemigaleus* Bleeker, 1852 because of dentition differences and lack of precaudal pits but he declined to establish a new genus for it.

Fowler (1941) overlooked *Eugaleus omanensis* in his review of Indo-Pacific elasmobranchs but later (1956) gave a description of the species condensed from Norman's account and allocated it to the genus *Galeorhinus*. Misra (1949) had earlier placed it in the same genus but this was not mentioned by Fowler.

Smith (1957) revised *Galeorhinus* but also overlooked *G. omanensis*. Compagno (1970) reviewed the systematics of *Hemistriakis*, *Galeorhinus*, and related genera. He considered *G. omanensis* generically distinct from *Galeorhinus* but did not propose a new genus in deference to this paper.

During the International Indian Ocean Expedition (IIOE) in 1963, the RV *Anton Bruun* on Cruise 4B conducted 109 trawling stations in transects along the continental shelf of the Arabian Sea between Bombay and the Gulf of Oman at depths from 15 to 375 m (Woods Hole Ocean-

ographic Institution, 1965). Sixteen specimens of a small carcharhinid were included in these collections and sent to us through the Smithsonian Oceanographic Sorting Center. They were tentatively identified by us as *Galeorhinus omanensis* (Norman).

Marshall and Bourne (1964, 1967), in photographic surveys of benthic fishes, collected 30 photographs of a small carcharhinid shark (about 2 ft long) at depths between 1115 and 2195 m in the Red Sea. They noted that their shark might be either a triakid or a carcharhinid but was not identifiable to genus or species. Comparison of Marshall and Bourne's photographs and sketch of their "mystery shark" with our specimens and Norman's account of *G. omanensis* led us to suspect that the "mystery shark" might be *omanensis*.

We then sent two specimens of the IIOE series to Dr. N. B. Marshall at the British Museum (Natural History). At our request he compared them with the holotype, the hitherto only known specimen of *Galeorhinus omanensis*, and confirmed our identification of the IIOE specimens. He also agreed that the IIOE *omanensis* are very similar to the Red Sea "mystery shark" of the photographs, but noted that final identification of the Red Sea species must await capture of specimens.

Differences between "*Galeorhinus*" *omanensis* and members of *Galeorhinus*, *Hypogaleus*, *Hemistriakis*, and all other carcharhinid genera warrant the erection of a new genus for "*Galeorhinus*" *omanensis*.

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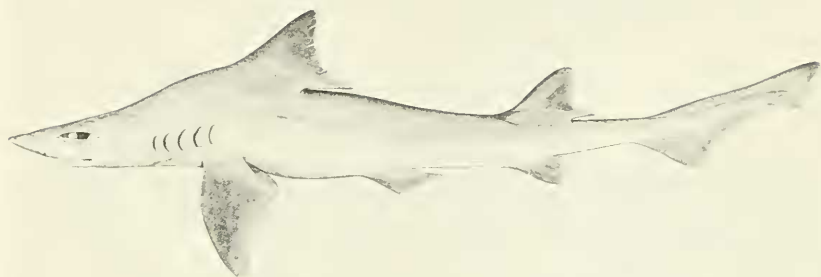


FIGURE 1.—*Iago omanensis*, from a 565-mm female deposited in U.S. National Museum. Drawing by Mildred H. Carrington.

Iago GENUS NOVUM

Eugaleus omanensis NORMAN, 1939,
TYPE-SPECIES

Etymology

This shark, a namesake of the villain of Shakespeare's *Othello*, is a troublemaker for systematists and hence a kind of villain.

Diagnosis (Terminology Follows Compagno, 1970)

Iago (Figure 1) differs from most carcharhinoids in the extremely anterior origin of its first dorsal fin. Only *Isogomphodon oxyrinchus*, a few species of *Carcharhinus*, and the sphyrid *Eusphyra blochii* rival *Iago* in this respect.

Iago is morphologically intermediate between the families Triakidae and Carcharhinidae as defined by Bigelow and Schroeder (1948) and Garrick and Schultz (1963). The characters of *Iago* strengthen the evidence presented by Compagno (1970) against separation of these families on simple nictitating lower eyelid and dental characters advocated by these writers.

We follow Compagno in uniting, at least provisionally, the two families. *Iago* thus falls into the family Carcharhinidae (sensu lato).

Iago is far from the advanced and intermediate carcharhinid genera discussed by Compagno (1970). These genera include *Hemigaleus*, *Hemipristis*, *Galeocerdo*, *Scoliodon*, *Rhizoprionodon*, *Loxodon*, *Negaprion*, *Triaenodon*, *Lamiopsis*, *Isogomphodon*, *Carcharhinus*, *Hypoprion*, and *Aprionodon*. *Iago* differs from all of these in having a transitional, not internal, nictitating lower eyelid with edge nearly horizontal; shallow subocular pouch; teeth with strong basal ledges and grooves; teeth at symphysis only slightly smaller than adjacent ones; no precaudal pits; pectoral fin skeleton projecting less than halfway into fin; distal pectoral radials only as long as proximals, with parallel edges and truncate tips (not tapered and acute); caudal fin without projecting ventral lobe and lateral undulations of its dorsal margin in adults; cranium with a complete supraorbital crest (absent in advanced forms); and a spiral, not scroll, intestinal valve (*Hemigaleus* and *Hemipristis* are exceptional in also having spiral valves).

Iago differs from *Galeorhinus* and *Hypogaleus* as delimited by Compagno (1970) in having a transitional rather than internal nictitating low-

er eyelid in adults, with nearly horizontal edge; anterior nasal flap not greatly reduced; teeth without postlateral cusplets; an interdorsal ridge present; lateral trunk denticles much longer than wide in adults (about as long as wide in *Hypogaleus* and *Galeorhinus*); and no ventral lobe on caudals of adults.

From the curious *Leptocharias*, *Iago* differs in having a transitional rather than internal nictitating lower eyelid in adults; much larger spiracles; no nasal barbel; very weak gynandric heterodonty; teeth with primary cusps oblique, not erect, and lacking cusplets; sharp-edged, bladellike cutting teeth; fewer total vertebrae, 130 to 147 (198 to 214 in *Leptocharias*); spiral intestinal valve with about 5 turns (14 to 16 in *Leptocharias*); and an entire supraorbital crest (reduced in *Leptocharias* to isolated preorbital and postorbital processes).

Iago can be distinguished from *Hemitriakis*, *Furgaleus*, *Scylliogaleus*, the *Triakis-Mustelus* complex, *Proscyllium*, and *Eridacnis* by its more lateral eyes, in dorsal view nearly touching head rim, and its sharp-edged, monocuspidate teeth. In addition, *Iago* differs from *Hemitriakis* in having a transitional rather than external nictitating lower eyelid, noncarinate posterior teeth, more tooth rows (only 18 to 36 29 to 34 in *Hemitriakis*), weak transverse notches on teeth, and no ventral caudal lobe. *Iago* lacks the short, thick, rounded snout, nasoral grooves, and molariform teeth of *Scylliogaleus* and also has fewer tooth rows and series of teeth functional. Unlike *Furgaleus*, *Iago* lacks nasal barbels, erect cusps on its lower anterolateral teeth, and a ventral caudal lobe; also, *Iago* (Figure 2) has the nostrils definitely closer to the mouth than the snout tip (about equidistant in *Furgaleus*). *Iago* differs from most members of the *Triakis-Mustelus* complex in having fewer tooth rows and series of teeth functional; however, *Triakis semifasciata* rivals *Iago* in these respects. *Iago* does not have a pavement of molariform teeth as in *Mustelus*; also, its pelvic anterior margins are less than half the length of pectoral anterior margins (over half as long in *Triakis-Mustelus*). Finally *Iago* contrasts with *Proscyllium* and *Eridacnis* by its transitional, not rudimentary, nictitating lower eyelid; monocuspidate poster-

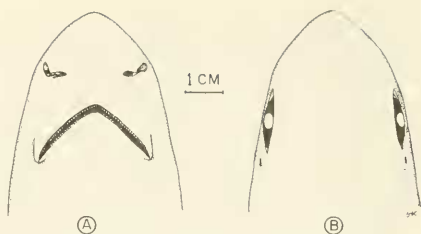


FIGURE 2.—*Iago omacensis*. A. Ventral side of head. B. Dorsal side of head.

ior teeth (not comblike); dorsal fin base midpoint closer to pectoral base termination than pelvic origins (vice-versa in *Proscyllium* and *Eridacnis*); second dorsal origin anterior (not over or posterior) to anal fin origin; intermedialia of vertebral centra strong wedges (not wedgelike in *Proscyllium* and *Eridacnis*); large papillae absent from gill arches and buccal cavity; and nostrils farther apart. *Iago* also lacks the clasper hooks, scyliorhinoid color pattern, and apparently the oviparous reproduction of *Proscyllium*.

GENERIC DESCRIPTION

Head flattened, its length from snout tip to fifth gill opening about $\frac{1}{4}$ total length.

Eye openings dorso-lateral, not visible in ventral view of head, openings elongate, about twice as long as high, with a well-developed posterior notch; nictitating lower eyelid transitional (Figure 3B), its edge nearly horizontal; secondary lower eyelid strongly differentiated, its edge thin; subocular pouch shallow, its lateral surface bare of denticles.

Slitlike spiracles, length about $\frac{1}{4}$ eye length, located about $\frac{2}{3}$ eye length behind and slightly below posterior eye notch; external gill slits moderately short, lengths in adults nearly equal, the longest $\frac{1}{2}$ to $\frac{2}{3}$ eye length; nostrils located about one-half as far from mouth as from snout tip, well separated, without nasoral grooves, widths about $1\frac{1}{2}$ to 2 times internarial distance, anterior nasal flap a short truncate lobe.

Mouth opening subtriangular, broad, 2 to 2½ times as wide as long; labial furrows extending around mouth corners, the upper furrows longer, extending anteriorly only to below eye pupils; large papillae absent from buccal cavity.

Teeth small (Figures 3A and 4), largest with greatest width at root about 1.5 mm in 457-mm female; tooth rows 46 to 55/37 to 45; 2 to 3 series functional along edges of jaws; teeth in mixed alternate and imbricate overlap pattern of Strasburg (1963); no serrations; premedial edge of crown in anteroposteriors convex, post-lateral edge deeply notched forming a low post-lateral blade on crown foot; all teeth with a strong basal ledge and groove, transverse ridges on crown foot; roots low, deep, with transverse

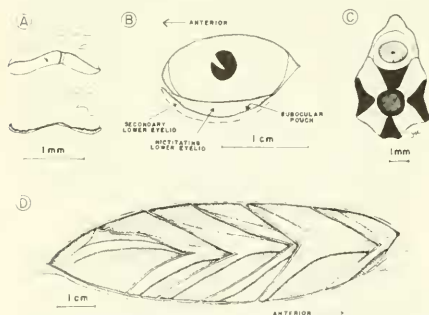


FIGURE 3.—*Iago omanensis*. A. Typical teeth: upper, buccal surface; lower, labial surface. B. Eye. C. Cross section of trunk vertebra; thoroughly calcified areas shown in black. D. Valvular intestine, one side cut away. Drawing by L. J. V. Compagno.

groove on attachment surface but transverse notch weak; teeth not noticeably protruding when mouth is closed.

Dignathic heterodonty very weak, with upper anteroposteriors having slightly higher crowns than lower ones; disjunct monognathic heterodonty indicated by differentiation of medials in one row on upper jaw and about 3 in lower; medials smaller, with erect primary cusps, large premedial and postlateral blades, and no cusplets; larger anteroposteriors are sharp-edged, compressed, bladelike cutting teeth with an oblique



FIGURE 4.—*Iago omanensis*. Teeth of right side of upper and lower jaws; labial aspect. Dotted lines indicate jaw symphysis.

primary cusp and no cusplets; anteroposteriors show moderate gradient monognathic heterodonty, with teeth becoming smaller, more oblique-cusped, and lower-crowned towards ends of dental band; posteriormost teeth with strong primary cusps; ontogenic heterodonty not known at present; gynandric heterodonty indicated only by slightly more erect cusp tips on anteroposteriors of adult males.

Trunk not markedly compressed, less than twice as high as wide, subtriangular in cross section; a low interdorsal ridge present; lateral dermal keels and precaudal pits absent from caudal peduncle.

Dermal denticles of trunk below first dorsal longer than wide, crown with a high, narrow ridge extending to tip of posteriorly directed cusp; a pair of lateral ridges weakly developed or absent, lateral cusps weak or absent.

Pectoral fins larger than first dorsal fin in area, their anterior margins about 1½ times as long as combined base and inner margin lengths; distal tip of adpressed pectoral about over its free rear tip when pectoral inner margin is held parallel to body axis; origin of pectoral below or slightly in advance of fourth gill opening; pectoral skeleton projecting less than halfway into fin, its longest distal radials about equal in length to corresponding proximal ones; distal radials with truncate tips and parallel edges.

Pelvic anterior margins less than half length of pectoral anterior margins; pelvic bases equidistant between first and second dorsal bases.

Claspers with pseudoperae, pseudosiphons, cover rhipidia, true rhipidia, and exorhipidia (Figures 5B and 5C); siphon sacs large, extending anteriorly to level of pectoral free rear tips (Figure 5A); margins of clasper cartilage rolled, with margins overlapping to form a tube; clasper hooks absent.

Origin of first dorsal fin far forward, varying in position from above fourth gill opening to slightly before pectoral axilla; midpoint of first dorsal base much closer to pectoral axilla than to pelvic origins; free rear tip of first dorsal anterior to pelvic fin origins.

Second dorsal nearly as large as first, its height about 70% of first dorsal height; its posterior margin strongly concave.

Anal smaller than second dorsal, slightly more than half its height, its base about $\frac{2}{3}$ of second dorsal base length; its posterior margin nearly straight or shallowly concave; its origin posterior to second dorsal origin by about $\frac{1}{5}$ of second dorsal base length; posterior ends of second dorsal and anal bases opposite.

Caudal without projecting ventral lobe-tip in adults, preventral margin slightly more than $\frac{1}{3}$ of dorsal margin length; subterminal margin long, over half length of terminal margin; caudal dorsal margin length about $\frac{1}{5}$ of total length; terminal sector of caudal about $\frac{1}{3}$ of dorsal margin length; vertebral axis of caudal only slightly raised above body axis.

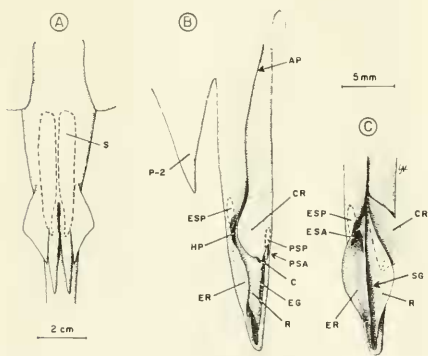


FIGURE 5.—*Iago omanensis*. A. Ventral aspect of trunk of mature male to show size and position of clasper siphons. B. Dorsal surface of left clasper. C. Partially expanded tip of left clasper. AP, apophysis; C, connection between rhipidion and cover rhipidion; CR, cover rhipidion; EG, epirhipidial groove; ER, epihypopodial; HP, hypopyle; P-2, pelvic fin; ESA, pseudoperopod aperture; ESP, pseudoperopod; PSP, pseudosiphon pouch; R, rhipidion; S, siphon sac; SG, subrhipidial groove.

Vertebrae moderately numerous, 129 to 147 in total count ($N = 16$). Monospondylous precaudal (MP) centra 24.5 to 27.6% of total count; diplospondylous precaudal (DP) centra 33.6 to 36.1; and diplospondylous caudal (DC) centra 37.2 to 40.1 ($N = 8$). A ratios 120 to 162, B ratios 102 to 137 ($N = 11$). DP and DC centra more numerous than MP centra and nearly equal to each other, DP/MP ratio 1.22 to 1.46 and DC/MP ratio 1.38 to 1.63 ($N = 8$). Transition between MP and DP centra easily delimited on radiographs, over pelvic region. Posteriormost MP centra not greatly hypertrophied. DP centra of relatively uniform length throughout, not forming a stutter zone of alternating long and short centra.

Vertebral calcification pattern a modified version of White's (1937) "Maltese cross" pattern, without diagonal calcified lamellae; notochordal canal unusually large (Figure 3C); wedgelike intermedialia strongly developed.

Supraorbital crest of cranium strongly developed and entire.

Intestinal valve of spiral type, with about five turns.

Iago is apparently livebearing (see section in Reproduction below), but whether or not a yolk-sac placenta is formed cannot be determined from available specimens.

Iago omanensis (NORMAN, 1939)

Eugaleus omanensis Norman, 1939, p. 11, Fig. 3 (type-locality, Gulf of Oman); Compagno, 1970 (generic systematics).

Galeorhinus omanensis Misra, 1949, p. 21 (in list of Indian elasmobranchs, name only); Fowler, 1956, p. 17 (description, after Norman); 1967, p. 363 (in list of fishes of the world, name only).

MATERIAL

Seven males, 224 to 365 mm; nine females, 358 to 582 mm (Table 1); holotype, British Museum (Natural History) Reg. No. 1939.5.24.9, a 280-mm female from Gulf of Oman. Speci-

TABLE 1.—Oceanographic data for *Iago omanensis* from Final Cruise Report, Anton Bruun Cruise 4B, Woods Hole Oceanographic Institution (1965).

Length of specimen	Sex	HOE station number	Date	Lat N	Long E	Bottom temperature	O ₂ at bottom	Depth
mm						° C	ml/liter	m
312	♂	227A	11/19/63	22°38'	67°11'	22.39	0.77	110
224	♂	231A	11/20/63	23°13'	66°40'	19.89	0.24	183-155
457	♀	255A	11/30/63	25°50'	57°07'	24.47	2.40	92-95
427	♀	255A	11/30/63	25°50'	57°07'	24.47	2.40	92-95
440	♀	264A	12/02/63	25°02'	56°52'	20.02	0.60	291-272
480	♀	264A	12/02/63	25°02'	56°52'	20.02	0.60	291-272
472	♀	264A	12/02/63	25°02'	56°52'	20.02	0.60	291-272
363	♂	264A	12/02/63	25°02'	56°52'	20.02	0.60	291-272
358	♀	268A	12/03/63	24°12'	57°26'	16.24	0.28	364-368
565	♀	268A	12/03/63	24°12'	57°26'	16.24	0.28	364-368
582	♀	268A	12/03/63	24°12'	57°26'	16.24	0.28	364-368
335	♂	268A	12/03/63	24°12'	57°26'	16.24	0.28	364-368
365	♂	268A	12/03/63	24°12'	57°26'	16.24	0.28	364-368
395	♀	279B	12/09/63	24°13'	65°52'	19.34	0.22	170-192
304	♂	279B	12/09/63	24°13'	65°52'	19.34	0.22	170-192
295	♂	279B	12/09/63	24°13'	65°52'	19.34	0.22	170-192

mens are deposited in the collections of the U.S. National Museum, California Academy of Sciences, and the British Museum (Natural History).

DESCRIPTION

Proportional dimensions as percentages of total length are given for our 16 specimens in Table 2.

In lateral view head outline slightly convex dorsally and ventrally, its outline tapering smoothly to snout tip; outline of head in dorsal view parabolic in shape, the sides converging at a narrow angle from gill openings to nostrils but then converging at a much wider angle to snout tip; head broad, width at spiracles about half its length; interocular slightly less than width of head at eyes; head subquadrate in transverse section at eye pupils.

Snout tip narrowly rounded in dorsal view, bluntly pointed in lateral view; preoral length 1.1 to 1.4 in mouth width.

Eye length equal to or slightly longer than distance between nasal apertures; eye openings subelliptical, rounded anteriorly.

Nictitating lower eyelid (NLE) a variety of Compagno's (1970) transitional type, intermediate in form between "nictitating folds" and "nictitating membranes" of authors (Figure 2B); its anterior edge smoothly confluent with

edge of upper eyelid; secondary lower eyelid (SLE) originating beneath origin of NLE; posteriorly NLE merges with SLE and continues as single edge to notch; subocular pouch or pocket between NLE and SLE extends beneath anterior two-thirds of eye; SLE edge sharp and thin with NLE is artificially raised to the limits of its travel; dermal denticles present on outer face of NLE. The structure and the kinetics of the NLE in *Iago omanensis* suggest that it cannot cover the posterior third of the eye when raised as it can in adults of *Galeorhinus* and higher carcharhinoids.

Spiracles open below level of posterior eye notch and are posterior to eye by distance about equal to their own length.

Gill openings increasing in size from first to third by small increments, with fourth slightly shorter than third and fifth about half length of fourth, becoming more dorsally situated from anterior to posterior, with upper origin of first opposite midpoint of fifth. Definite gill rakers not developed, but small dermal mounds are present on gill arches.

Nostrils relatively large, their openings obliquely directed anterolaterad; anterior nasal flap varying from subtriangular to lobate; a small inner nasal flap present dorsal to anterior nasal flap and concealed by it; posterior nasal margin with an elongated process (stiffened by ala nasalis) that projects obliquely dorsomedially into nasal cavity.

TABLE 2.—Proportional measurements of *Iago omanensis* expressed as percentages of total lengths; measurement method follows Bigelow and Schroeder (1948).

	Male 335 mm	Range in 7 males	Female 565 mm	Range in 9 females
Tip of snout to:				
Front of mouth	7.2	6.1-7.6	5.8	5.7-6.4
First gill opening	19.1	17.4-20.0	16.8	16.2-17.8
Last gill opening	24.2	24.2-27.5	23.4	23.0-24.5
Origin pectoral fin	23.3	23.3-25.9	22.7	21.2-23.5
Origin first dorsal fin	25.9	25.3-29.5	24.8	24.0-27.1
Origin pelvic fins	42.8	41.6-45.9	43.9	42.7-46.5
Origin second dorsal fin	56.8	56.8-60.6	58.4	57.8-59.9
Origin anal fin	58.3	58.3-63.4	59.2	59.2-63.3
Anus	44.7	43.5-49.1	45.1	44.5-47.4
Distance between fin base:				
First and second dorsals	23.5	21.4-25.3	24.2	21.9-24.6
Pectoral and pelvic	16.1	13.7-16.1	18.6	16.8-20.0
Pelvic and anal	11.0	11.0-12.3	11.5	11.0-13.2
Anal and lower caudal	8.9	7.2-10.5	8.5	7.5-9.7
Length eye opening	5.1	4.2-5.1	4.1	3.3-4.1
Least internasal distance	4.0	3.6-4.2	3.7	3.3-3.9
Width mouth	7.2	7.7-9.4	7.1	6.4-8.4
Length upper labial furrow	1.5	1.5-2.0	1.2	1.1-1.2
Length lower labial furrow	0.9	0.8-1.4	0.9	0.6-1.1
Diameter spiracle	0.6	0.4-0.8	0.5	0.2-0.6
Distance, spiracle to eye	0.7	0.7-1.1	1.1	0.7-1.2
Fin measurements:				
Base first dorsal	8.9	8.9-11.2	9.4	8.3-11.6
Height first dorsal	6.0	6.0-7.8	7.8	7.0-8.8
Base second dorsal	8.9	8.0-9.7	7.3	7.3-9.1
Height second dorsal	4.8	4.5-6.1	5.5	5.2-6.5
Base anal	6.0	5.5-6.6	5.3	4.9-6.4
Height anal	3.0	2.6-3.4	3.5	2.8-4.0
Width pectoral base	4.8	4.7-5.6	4.8	4.5-5.6
Anterior margin pectoral	14.3	12.7-14.3	15.3	13.4-16.6
Overall length pelvics	8.6	8.3-9.9	9.6	8.5-9.6
Upper margin caudal	22.4	20.1-22.4	21.9	20.8-22.7

¹ In 4 males or 6 females.

Mouth width about two-thirds of width of head at mouth corners; edge of lower jaw convex.

Teeth show modest gradient heterodonty; from symphysis to mouth corner teeth become lower relative to their root lengths; tooth size changes also along this gradient, starting from small to largest in about four rows from medials and gradually becoming smaller towards ends of dental band.

Body moderately slender, trunk rather high anteriorly, almost humped above pectorals, sloping posteriorly to pelvics and caudal origins; caudal peduncle long, slender, subquadrate in cross section, a weak postdorsal ridge extending medially from just after second dorsal to caudal origin; an ill-defined predorsal ridge extending for a short distance anterior to first dorsal fin; distance from snout tip to cloaca somewhat less than distance from cloaca to caudal tip.

Dermal denticles small, those of dorsal surface below first dorsal fin base 0.04 to 0.08% of total length in two specimens, 0.15 to 0.35 mm in 457-mm female; anterior edges and posterior cusps of adjacent denticles somewhat overlapping, skin visible between denticles; denticles transparent, without pigment and more or less invisible when wet; chromatophores of skin between denticle bases visible through denticles; bases of denticles short, subquadrate, with relatively short pedicels; medial ridge of crown not subdivided longitudinally (Figure 6); concave depression present on either side of medial ridge, with its lateral boundary deflected slightly outward to form an incipient lateral ridge that may or may not terminate in a short lateral cusp; lateral cusps generally absent from denticles of caudal and ventral surfaces; denticles below first dorsal becoming wider relative to their lengths with increase in specimen size; small denticles

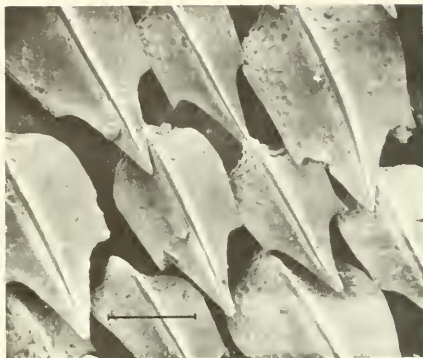


FIGURE 6.—*Iago omanensis*. Dermal denticles from side of trunk below first dorsal fin, 582-mm female, scanning electron microscope photomicrograph, scale line at lower left equals 100 μ .

(less than 0.1 mm long) present on anterior part of palate and inner surfaces of branchial arches, also irregularly and rather sparsely scattered on tongue.

Pectoral fins broad, subangular, with their anterior margins convex, apices rounded, posterior margins slightly convex, free rear tips rounded, and inner margins convex, relatively short, their anterior margins about an eye diameter shorter than distance from snout tips to first gill opening; pectoral inner margins long, about $1\frac{1}{2}$ to $1\frac{2}{3}$ times pectoral base length; posterior margin about $1\frac{1}{3}$ to $1\frac{1}{2}$ times in anterior margin; free rear tip of pectoral varying in position from below posterior end of first dorsal base to last third of first dorsal base.

Pectoral fin skeleton, as studied on radiographs, somewhat similar to that of *Galeorhinus*; propterygium with 1 radial, mesopterygium with 3 or 4, segmented metapterygial axis with 10 to 12; metapterygial axis elongate, much larger than anterior basals, with a distal set of segments; radials mostly divided into three segments (proximal, intermediate, and distal), intermediates shorter than proximals or distals, which are equal in length.

Pelvic fins somewhat larger than anal but smaller than second dorsal in area; pelvises in some males relatively smaller than those of females; pelvises triangular, with anterior margins slightly convex to nearly straight, apices broadly rounded to subangular, posterior margins nearly straight, free rear tips acute (slightly attenuate in some specimens), inner margins straight; pelvic anterior margins 2.6 to 2.8, posterior margins 1.7 to 1.9, and inner margins 1.4 to 1.6 in comparable margins of pectorals.

Claspers and associated secondary sexual structures of males generally similar in basic plan to those described for *Galeorhinus galeus* (as "*Galeus vulgaris*") by Leigh-Sharpe (1921), but differing in several details; claspers long, more slender and more angular distally than those of *Galeorhinus* with bluntly pointed, flattened tips (Figure 5A); claspers of adult males extending well beyond free rear tips of pelvis; clasper groove roofed over and closed by its overlapping sides from apophysis to hypophysis; small pseudosiphon present mediodorsally, its pouch extending anteriorly on clasper. Unlike *Galeorhinus*, the pseudosiphon aperture is much less prominent and is located relatively farther from the clasper tip. Cover rhipidion very large (scarcely developed in *Galeorhinus*), formed as a rounded flap completely covering rhipidion; rhipidion evenly rounded (wedge-shaped in *Galeorhinus*); pseudopoda present, dorsolateral and opposite to the rhipidion edge (as in *Galeorhinus*); unlike *Galeorhinus*, the pseudopoda is partially covered by another flap, here termed the exorhipidion, which originates laterad to the pseudopoda and extends posteriorly to cover part of the rhipidion. Hypophysis opening at level of pseudopoda, cover rhipidion, and anterior third of rhipidion.

Clasper skeleton studied from radiographs of six males. Terminology is modified from Jungerson (1899) and White (1936, 1937). One basal cartilage connecting clasper cartilage to pelvic basiptyrgium; a small beta cartilage present at the junction of basal cartilage and clasper cartilage; details of terminal cartilages not clear, but at least two terminals, a dorsal and a ventral, are present; clasper cartilages heavily calcified in adult males.

First dorsal fin triangular with height much less than length from origin to free rear tip; origin ill-defined, grading into predorsal ridge; anterior margin slightly concave basally but convex towards fin apex, with a 45 degree slope relative to body axis; apex acutely rounded, posterior margin somewhat concave, free rear tip slender, elongate, acute; base much longer than fin height, inner margin about 60 to 70% of fin height; end of first dorsal base about over adpressed apex of pectoral; pectoral free rear tip anterior to pelvic origins by a distance nearly or quite equal to lengths of pelvic bases.

Second dorsal fin generally similar in shape to first dorsal; its height about half length from origin to free rear tip; fin base about 1.4 to 1.5 times height; inner margin about 0.5 to 0.7 of height; origin of second dorsal posterior to mid-point between anal origin and posterior end of pelvic base; free rear tip of second dorsal opposite or slightly posterior to that of anal; second dorsal over twice area of anal.

Anal fin a low triangle, with height about 0.4 in length, anterior margin broadly convex, apex rounded, posterior margin moderately concave, free rear tip slender and acute, and inner margin concave; inner margin almost or quite equal in length to height; fin base 1.4 to 1.6 times fin height.

Dorsal margin of caudal nearly straight, pre-ventral margin broadly convex, and junction of pre-ventral and post-ventral margins rounded; post-ventral margin long, concave anteriorly but nearly straight posteriorly and curving abruptly upward into subterminal notch; subterminal margin nearly straight, terminal margin invariably frayed but apparently moderately concave.

Vertebral counts given in Table 3.

Vertebral calcification pattern was studied from transverse sections and radiographs of centra from below first dorsal fin. Terminology for vertebral parts follows Ridewood (1921). Primary double cone without diagonal calcified lamellae; solid dorsal, lateral, and ventral inter-medialia present, separated by uncalcified areas for the basidorsals and basiventrals (Figure 3C); notochordal canal at constricted portion of double cone unusually large (as in many other

deepwater sharks, a feature possibly correlated with habitat).

The chondrocranium was dissected out in one specimen but is not described here. It is similar in structure to the crania of *Galeorhinus* and *Mustelus* described by Gegenbaur (1872) but differs in numerous details from both.

Stomach very large, subdivided into a sack-like fundus and a long slender pylorus. The fundus extends posteriorly over two-thirds the length of pleuroperitoneal cavity, then reverses direction as the pylorus to continue anteriorly nearly to root of liver, where it joins the spiral intestine. The latter is fusiform, with a spiral valve of about five turns (Figure 3D). The narrow rectum has a slender rectal gland attached distally to the epigonal organ in both sexes. Liver only moderately large, with paired lateral lobes concealing small medial lobe, posterior ends of lateral lobes extending only one-half to two-thirds of distance to posterior end of pleuroperitoneal cavity. Spleen elongate, not nodular, originating dorsally on distal end of fundus and coursing anteroventrally on pylorus to spiral intestine, where it extends posteroventrally to below the first intestinal valve. Pancreas elongate,

TABLE 3.—Vertebral numbers in male and female *Iago omanensis*.

Monospondylous precaudals	Diplospondylous precaudals	Caudal vertebrae	Total vertebrae
Males			
34	48	48	130
34	47	48	129
36	49	58	143
36	47	52	135
37	49	51	137
37	45	51	133
37	51	44	132
Females			
37	51	50	138
37	47	50	134
37	51	58	146
37	51	52	140
37	51	50	138
38	51	51	140
38	51	51	140
39	52	53	144
42	49	56	147

single, located anterior to spiral intestine and dorsal to stomach. Ovaries well-developed only on right side, with long epigonal organ extending posteriorly to rectal gland; both oviducts well-de-

veloped and functional in all adult females examined, with small nidamental glands almost obsolete on the right side in some specimens; both testes apparently functional, subequally developed in three males examined, with a single epigonal organ attached to left testes. Semilunar valves of conus arteriosus in two rows, the anterior one with three valves, the posterior with three much smaller valves located each on the posterior base of an anterior valve.

Color brownish or grayish above and lighter below, with no conspicuous markings or abrupt color changes from dorsal to ventral; expanded chromatophores in the darkest specimen give a peppered appearance; small areas of darker pigmentation present near tips of both dorsal and caudal fins and in some specimens extending along leading edges of fins; lining of buccal cavity and peritoneum whitish.

VARIATION

The variation in morphometrics among our 16 specimens is substantial, unusually so for a series of adult sharks. Most of the differences do not follow sex, but it is apparent that the abdominal section is longer in females than in males. Thus the distance between pectoral and pelvic bases ranges from 13.7 to 16.1% of total length in seven males but is 16.8 to 20.0% in nine females. This is similar to the situation reported for the squaloid *Euprotomierus bispinatus* by Hubbs, Iwai, and Matsubara (1967) and in *Carcharhinus leucas* by Thorson, Watson, and Cowan (1966). Large variations in tooth row and vertebral counts were noted also. Despite the range of variation between individuals and the sexual dimorphism in our sample, we find nothing to indicate that more than one species is represented or that the variation can be attributed to known geographical or environmental influences.

REPRODUCTION

One 440-mm specimen in our series has partially developed and uncalcified claspers but has eggs with very early embryos in the oviducts.

Thus the specimen is, at least functionally, a female. Histological examination of the ovaries was not made, but gross examination revealed one ripe ovary of normal appearance but little development of the other gonad. A similar instance of the partial development of claspers by a functional female *Centrophorus lusitanicus* was reported by Cadenat (1960). A more extreme example, recorded by King (1966), was of a hermaphroditic *Scyliorhinus caniculus* with a single immature clasper, a ripe ovotestis (with ovarian follicles at all stages and seminiferous tubules with mature sperm), and functional nidamental glands, oviducts, vasa deferentia, and seminal vesicles (with sperm). King also listed another *S. caniculus* specimen with two immature claspers, a ripe ovotestis, and oviducts, but no seminal vesicles and vasa deferentia. The opposite condition was found in a field-dissected specimen of *Mustelus higmani* by Dr. John Thompson (Springer and Lowe, 1963). This individual lacked claspers but had a pair of enlarged testes.

It may be significant that in the above cases the size of each shark was within the range of its functional sex at maturity regardless of external characters belonging to the opposite sex. The *Iago* and *Centrophorus* females with claspers were larger than would be expected for mature males of the species, but the clasperless male *Mustelus* was smaller than mature females of its species. Both hermaphroditic *Scyliorhinus* were the size of adult females of their species despite the presence of claspers.

Our smallest male, 224 mm long, is immature with uncalcified claspers but six others from 295 to 363 mm are mature. We did not examine internally a 358-mm female, the smallest of its series, but eight others from 395 to 582 mm are mature and have eggs in their oviducts. The eggs are for the most part not large, having yolks not more than 10 mm in diameter, and in our specimens, embryos, when present, are in a very early stage of development. In the oviducts each egg is encased in a thin and soft membranous shell which closely adheres to the oviduct lining. The nidamental glands vary in size from scarcely visible enlargements of the anterior oviduct to about 10 mm in diameter,

but all are far smaller than those present in oviparous scyliorhinids. The condition of nidamental glands and eggshells indicate that *Iago omanensis* is livebearing, with oviductal egg counts suggesting a litter of 2 to 10 young. The relatively small size of egg yolks implies that a maternal source of nourishment is provided the embryos unless the young are extremely small at birth.

SIZE

Iago is one of the smaller carcharhinids. In the Carcharhinidae, *Scoliodon*, the *Protozygaena* group in *Rhiodoprionodon*, and *Mustelus* have species nearly or quite as small as *I. omanensis*, though *Eridacnis* species are even smaller. One of the latter, *E. radcliffei*, is apparently the smallest carcharhinid and one of the smallest sharks, with males mature at 186 mm and females at 216 mm.

Size disparity between the sexes is a common phenomenon among elasmobranchs, in all known cases with females larger than males. In *Iago omanensis* this disparity is very marked; our largest male (365 mm) was only 63% as long as the corresponding female (582 mm) and weighed but one-sixth as much.

FOOD

Stomachs of two specimens contained remains of unidentified fish, in one a fish head 32 mm long and in the other a 50-mm section of the posterior trunk of a fish estimated to have been more than 200 mm long.

DISTRIBUTION

Table 1 shows the distribution of 16 of 17 known specimens of *Iago omanensis*, all except the holotype from IIOE Cruise 4B. Only three other shark specimens, all *Mustelus* sp., were collected during Cruise 4B from 81 trawling stations in the northern Arabian Sea. This total of only 19 shark specimens of two species is much lower than the expected catch for comparable gear in many other areas of continental shelf and slope.

A possible explanation for the low incidence of sharks in the catches lies in frequent presence

of poorly oxygenated water near the bottom along the coast between the Gulf of Kutch and the Gulf of Oman (See Banse, 1968, for a general account of the hydrography of part of this area). Sharks of species commonly held in marine aquaria are thought to require a high dissolved oxygen level for survival although studies to verify this for particular species have not been made.

Low oxygen concentration in water at the bottom, 0.22 to 0.77 ml/liter, is associated with five of the six IIOE stations at which *Iago omanensis* was taken. It appears that this species may be exceptionally tolerant to low oxygen levels, even at the moderately warm (16.24° to 22.39° C, or about 61.3° to 72.4° F) water it apparently inhabits. In the Red Sea, Marshall and Bourne (1964) reported that their unidentified carcharhinid (which may be *Iago omanensis* or a close relative) occurred at depths down to 2195 m. As this area and these depths may have oxygen concentrations lower than 1 ml/liter at the end of summer (Richards, 1957), the Marshall and Bourne shark may be able to survive oxygen levels as low as known *Iago omanensis* apparently does in the Arabian Sea.

Gibbs and Hurwitz (1967) regarded the greater development of gill lamellae in the stomiatoid fish, *Chauliodus pammelas* compared with that in *C. sloani* as an adaptation to the low oxygen habitat of *C. pammelas*. We looked at structures having respiratory functions in *Iago omanensis* but found nothing to suggest such an adaptation. *I. omanensis*, however, has no closely allied species as a basis for comparison.

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